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Modeling with Limited Data: The Influence of Crop Rotation and Management on Weed Communities and Crop Yield Loss

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Theory and models of crop yield loss from weed competition have led to decision models to help growers choose cost-effective weed management. These models are available for multiple-species weed communities in a single season of several crops. Growers also rely on crop rotation for weed control, yet theory and models of weed population dynamics have not led to similar tools for planning of crop rotations for cost-effective weed management. Obstacles have been the complexity of modeling the dynamics of multiple populations of weed species compared to a single species and lack of data. We developed a method to use limited, readily observed data to simulate population dynamics and crop yield loss of multiple-species weed communities in response to crop rotation, tillage system, and specific weed management tactics. Our method is based on the general theory of density dependence of plant productivity and extensive use of rectangular hyperbolic equations for describing crop yield loss as a function of weed density. Only two density-independent parameters are required for each species to represent differences in seed bank mortality, emergence, and maximum seed production. One equation is used to model crop yield loss and density-dependent weed seed production as a function of crop and weed density, relative time of weed and crop emergence, and differences among species in competitive ability. The model has been parameterized for six crops and 15 weeds, and limited evaluation indicates predictions are accurate enough to highlight potential weed problems and solutions when comparing alternative crop rotations for a field. The model has been incorporated into a decision support tool for whole-farm management so growers in the Central Great Plains of the United States can compare alternative crop rotations and how their choice influences farm income, herbicide use, and control of weeds in their fields.

Key words: Competition, crop rotation, density dependence, simulation, weed seed production.

Growers rely primarily on tactical tools, mainly herbicides, to control weeds and prevent yield loss, but crop rotation is an important strategic tool for weed management in some systems. Sequences of crops can be selected to use the most cost-effective tactical tools or to reduce weed seed production through crop characteristics such as competitiveness or a life cycle that prevents a weed from reaching maturity (Anderson 2005; Doucet et al. 1999). In 1997, USDA–ARS, in collaboration with Colorado State University, began developing a whole-farm and ranch management decision support system for strategic planning in the Great Plains. This system (GPFARM, Great Plains Framework for Agricultural Resource Management) was designed to assist growers with strategic planning by allowing them to test and compare alternative agricultural management systems. Early in the design of GPFARM, potential users indicated that weed management is one of the most important factors in their decisions about crop rotation. We needed to develop a model that predicted multi-year population dynamics and crop yield loss of multiple-species weed communities to incorporate weed management in strategic planning.

Both appropriate models and the data to parameterize models were a challenge for developing a weed model for GPFARM. Data on many aspects of weed ecology required to model weed population dynamics are difficult or time-consuming to gather, and detailed knowledge of population processes is limited to a few major weed species. Modeling weed population dynamics for decision support, beyond control of weeds by herbicides during a single season, has been rare. Mathematical models describing the lifecycles of major weeds have been developed in anticipation that they will have predictive power, although they have rarely been used for this purpose (Cousens and Mortimer 1995). These models predict changes in population density in response to both intrinsic factors, such as species characteristics, and extrinsic factors such as management. Most of these models are for a single species. Even so, use of the most simple of these models for a variety of crops and management practices is limited by lack of data for choosing the values of model parameters.

Simple models of crop yield loss due to weed populations are plentiful and have been judged appropriate to be included in decision support models for herbicide choice (Wilkerson et al. 2002). These model crop yield loss as a function of the composition and density of weed populations. However, finding parameters for even these simple yield loss equations has been challenging, given the range and combination of species that farmers encounter in their fields. Experimental data and expert opinion, in combination, have been used regularly to estimate the relative competitive ability of weed species as well as the efficacy of herbicides for many of the major weed management decision models. Likely, models and parameters derived from experimental data have been adjusted by expert opinion for more general or specific applications. This approach is appropriate given that these are decision support systems. The goal is predictions that are sufficiently accurate to "help a decision maker make a better decision than he/she would have otherwise." (Wilkerson et al. 2002).

For GPFARM, we needed to model multi-year population dynamics of weed communities, responding to tactical management as well as major crop management strategies such as tillage systems and crop rotation. We also needed to predict crop yield loss due to each year's simulated weed population. Population dynamics and yield loss had to be predicted for communities of multiple species of weeds and the first version of the model had to be parameterized for 15 annual weed species and six crops for conditions of the Central

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Table 1. Description of parameters for calculating population change and yield loss in WISDEM.

Variable	Units	Range	Definition	Description
ReproMax	plants/area	≥ 0	Maximum reproduction	Maximum possible number of next generation plants per unit area that can be generated from a population, given high weed density and no other species present
Srv	no units	$0 \rightarrow 1$	Survival	Proportion of seeds surviving in soil for an entire year
CI	no units	$0 \rightarrow 1$	Competitive Index	Reciprocal of number of plants required to cause the same competitive effect as one plant of the reference species, defined as $N50_x/N50_1$
A'	no units	$0 \rightarrow 1$	Cousens (1985a)	Maximum proportional yield loss to more competitive species as density of less competitive species approaches infinity; defines degree of asymmetry in competition between species
N50	plants/area	≥ 0	Density 50%	Plants per unit area of a species required to achieve 50% of asymptotic maximum yield per unit area in monoculture
A^*	no units	≥ 0	Cousens (1985a)	Raw value of A' before being adjusted to give the dominant species in the system an A' value of 1; from A^*mean with adjustment for time of emergence.
A^0	no units	≥ 0	Cousens (1985a)	Average value of A^* when crop and weed emerge at same time, used with relative emergence time to compute specific value of A^*
D_{crem}	date	Julian day	Date of crop emergence	Specific day of simulated crop emergence, from user-specified planting date plus estimated number of days between crop planting and emergence (an estimated parameter)
K	1/days	≥ 0		Shape parameter of logistic function used for computing emergence time dependence of A^*, equal to the number of days after crop emergence for the A^* value to decline to 27% ($= (1 + e)^{-1}$) of A^*_{max}
eff	no units	$0 \rightarrow 1$	Efficacy	Efficacy parameter for herbicide or tillage, giving the proportion of weed plants which are killed by the weed control operation. For herbicides, efficacy parameters are specific to weed–herbicide pairs, whereas for tillage a single efficacy value is applied to all weeds for a given tillage implement
$D_{wdstart}$	date	Julian day	Date of start	Month and day of the start of weed emergence, the same every year
p1	days	≥ 0	Parameter 1	First parameter of Weibull emergence curve, equal to number of days for emergence to equal 63% ($= 1 - e^{-1}$) of the total emergence
p2	no units	≥ 0	Parameter 2	Second parameter of Weibull emergence curve, directly proportional to the slope of the curve when $d = p1$
d_{comp}	days	≥ 0	Days to competition	Number of days between crop planting and computation of percent crop yield loss due to competition from weeds
POA	days	≥ 0	Period of activity	Number of days in which a soil-applied herbicide is active after the date of application
D_{wdmat}	date	Julian day	Date of weed maturity	Month and day of weed maturity, when the weed population reproduces and dies

Great Plains. Given the lack of appropriate models and data and the demanding requirements of a weed model for GPFARM, our intent was to model general trends in weed population density accurately enough to highlight potential weed problems and solutions when comparing alternative crop management for a field. Because conducting experiments for model development and parameterization was not realistic, our first design consideration was that the model had to be parameterized from existing information and expert opinion. The model we developed is both a component of GPFARM and an independent model called WISDEM (Weed Interference and Simple Demography Model) that is available at http://arsagsoftware.ars.usda.gov/agsoftware/. Here we describe our approach to predict changes in weed communities and crop yield loss with parameters that are easy to obtain and our first attempt to determine if the predictions are biologically reasonable.

Materials and Methods

Model Design. WISDEM builds on the model developed by Dunan et al. (1996) to predict the change in multiple-species weed communities with crop rotation, based on a small number of parameters that could be derived from literature sources and expert opinion. They combined a model that simulates weed management during a single season (Wiles et al. 1996) with a simple algorithm for weed population size change from year to year in response to level of weed control. The model's crop yield loss algorithm was built on the work of Lybecker et al. (1991) that demonstrated the use of expert opinion for derivation of crop yield loss parameters for tactical weed management decision support systems. WISDEM incorporates a more mechanistic weed population dynamics method (Population Change Model) than the model of Dunan et al. (1996) and includes a new method of computing crop yield loss due to weeds (Yield Loss Equation). In addition, WISDEM can be parameterized from a wider variety of literature sources in addition to expert opinion. Parameters of the Population Change Model and Yield Loss Equation are described in Table 1.

Population Change Model. The population change model of WISDEM is a simplification of the often-used model of the weed population life cycle illustrated in Figure 1. The cycle begins with the preseason seed bank of viable seeds for a given weed species ($SBpre_t$). As the growing season commences, seeds in the seed bank can encounter three different fates: emergence, death, or survival. A proportion (β_{emg}) of weed seeds germinate and emerge as seedlings, another proportion (β_{onsrv}) survive the growing season in the soil seed bank, and the rest are lost from the seed bank due to predation, decay, unsuccessful emergence, and other causes. The number of seedlings is shown as $Npot_t$, the potential number of weed plants during the growing season. Control measures kill a proportion (β_{ctrl}) of the weed seedlings, leaving surviving weed plants ($Nsurv_t$). At weed maturity, the surviving weed plants produce seeds and die. On average, each plant produces a number of seeds referred to as SRP, seed rain per plant, whereas the total population of new seeds is called seed rain (SR_t). These new seeds enter the seed bank and, along with seeds which remained unemerged and survived from the beginning of the season, form the postseason seed bank $SBpost_t$. A proportion (β_{offsrv}) of the seeds in the postseason seed bank might then survive the off-season to form the seed bank at the beginning of the next growing season ($Sbpre_{t+1}$).

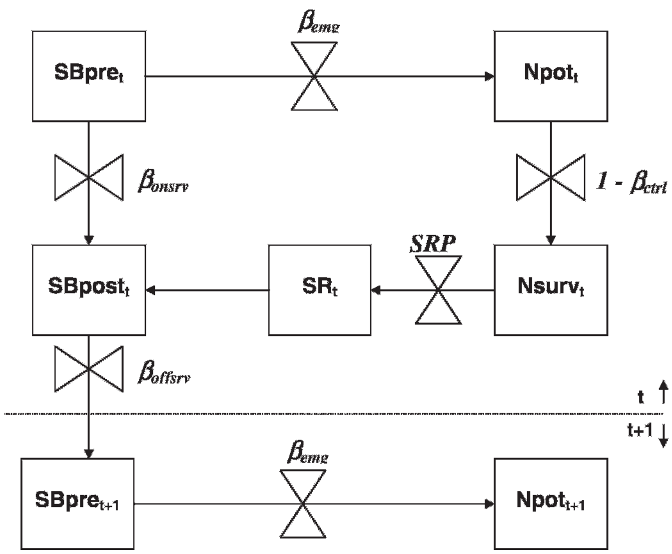

Figure 1. Flow diagram of a weed population dynamics model. Valves (double triangles) represent transition rate variables; rectangles represent state variables. Mathematically, if the arrow from Box1 points to Box2 via ValveA, then Box2 = Box1 · ValveA.

The off-season is defined as the period of time when the population exists only as seeds, with no living emerged plants. For summer annuals that emerge in the spring and mature in late summer or fall, the off-season is the winter. For winter annuals, which emerge in autumn and mature in summer, the off-season might only be a brief period during the summer.

Figure 1 can be represented by a single equation which gives potential emerged population (Npot) as a function of Npot in the previous year and several transition rate factors:

$$\mathrm{Npot}_t + 1 = \mathrm{Npot}_t \cdot \beta_{onsrv} \cdot \beta_{offsrv} + \mathrm{Npot}_t \cdot (1 - \beta_{ctrl}) \cdot \mathrm{SRP} \cdot \beta_{offsrv} \cdot \beta_{emg} \quad [1]$$

We simplified this model for WISDEM so that it requires estimating just two density-independent population transition parameters to model the processes represented by parameters β_{onsrv}, SRP, β_{offsrv}, and β_{emg}. Even with this simplification, seed rain per plant is density dependent and responds to the density of all species present in the system at the time of weed maturation.

Because seed rain SR = $\mathrm{Npot}_t \cdot (1\text{-}\beta_{ctrl}) \cdot \mathrm{SRP}$, Equation 1 can be rewritten as:

$$\mathrm{Npot}_{t+1} = \mathrm{Npot}_t \cdot \beta_{onsrv} \cdot \beta_{offsrv} + \mathrm{SR} \cdot \beta_{offsrv} \cdot \beta_{emg} \quad [2]$$

Density-dependent weed seed rain per unit area (SR) can be considered a curvilinear function that increases toward an upper asymptote as weed density increases, and decreases toward a lower asymptote as density of plants of other species increases (Watkinson 1981). Typically, an expression for this function would contain a term for the upper asymptote, i.e., the theoretical maximum seed rain, which can be called MaxSeed. The MaxSeed term can then be multiplied by a function ranging between zero and one, which describes the proportion of MaxSeed that is realized in a given density situation. We call this proportion PY_{weed} for proportional yield of the weed. The value of PY_{weed} must be a function of the surviving plant density of the weed in question (Nsurv_t), as well as the densities of the crop and any other weed species in the system. Thus, PY_{weed} incorporates the effects of weed control (β_{ctrl}) on weed seed rain. If SR is defined as MaxSeed · PY_{weed}, then Equation 2 can be rewritten as:

$$\mathrm{Npot}_{t+1} = \mathrm{Npot}_t \cdot \beta_{onsrv} \cdot \beta_{offsrv} + \mathrm{PY}_{weed} \cdot \mathrm{MaxSeed} \cdot \beta_{offsrv} \cdot \beta_{emg} \quad [3]$$

If it is assumed that MaxSeed is density independent and invariant over years, Equation 3 can be rewritten as:

$$\mathrm{Npot}_{t+1} = \mathrm{Npot}_t \cdot \mathrm{Srv} + \mathrm{ReproMax} \cdot \mathrm{PY}_{weed} \quad [4]$$

where Srv = $\beta_{onsrv} \cdot \beta_{offsrv}$ and ReproMax = $\beta_{emg} \cdot \beta_{offsrv}$ · MaxSeed.

Equation 4 is the core of WISDEM's population change algorithm, and the parameters of this equation can be estimated from the literature or expert opinion. This equation is a simplified formulation of the full model represented in Equation 2 and Figure 1, but is exactly equivalent to the full model in modeling situations where the full model parameters β_{onsrv}, β_{offsrv}, and β_{emg} are density independent and constant over years and SRP is density dependent but is based on a maximum seed production per plant (MaxSeed) that is constant over years. Because there is currently insufficient data on a broad range of weed species to be able to parameterize a model with β_{onsrv}, β_{offsrv}, β_{emg}, and MaxSeed varying over years, we think that this simplification is acceptable for purposes of WISDEM.

Yield Loss Equation. The proportional weed reproductive yield (PY_{weed}) describes the response of weed seed rain to the density of its own species, other weed species and the crop, and time of emergence relative to the crop. The value of PY_{weed} ranges between zero and one and represents the proportion of MaxSeed (the asymptotic maximum weed seed rain) which is produced in a given competitive situation. WISDEM must also predict crop yield loss in response to weed and crop density. Crop yield, like weed seed rain, can be predicted as proportional yield (PY_{crop}) that represents a proportion of the asymptotic maximum yield. We developed a single equation for WISDEM which can be used to express the relative yield of either a crop or a weed species as a function of the densities of all the other species in the system. This model was developed to reduce the number of parameters that would normally be required to model weed and crop yield. Usually, modeling crop yield requires one set of parameters whereas weed seed rain requires another completely different set of parameters.

The equation for proportional yield loss has not been validated for multiple species over a full range of densities because we have not found an applicable data set. We propose this equation for modeling crop and weed competition when there is a limited amount of actual experimental data. Complete derivation of this equation is beyond the scope of this paper, but the equation is derived from existing theory about density effects on plant productivity as described by hyperbolic models of crop yield loss (Cousens 1985a,b). The equation for proportional yield loss minimizes the number of required parameters by using the assumption that weeds use resources that otherwise would be used by the crop, leading to a roughly linear replacement of lost crop yield by increase in weed yield and vice versa (Canner et al. 2002).

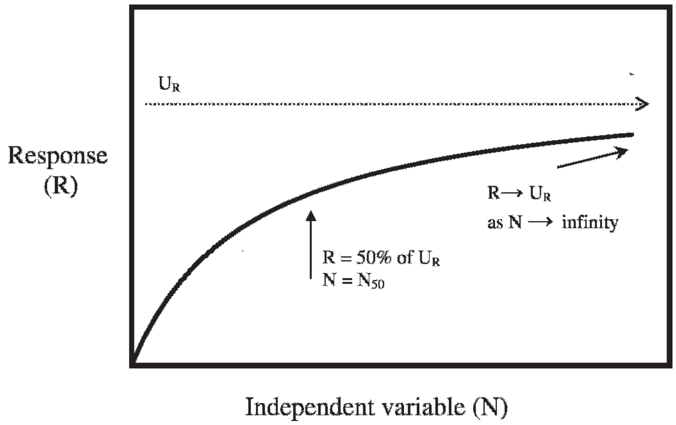

Figure 2. Simple rectangular hyperbolic function of the form $R = U_R \cdot (N/(N + N50))$, where R is the response being measured, U_R is the asymptotic maximum response level, N is the independent variable, and N50 is the level of the independent variable where 50% of U_R is achieved. The function has a horizontal asymptote at U_R, where R approaches U_R as N approaches infinity.

Yield Loss Equation: Density. The theoretical basis of the PY equation is described briefly in this section for the case of a crop with a single weed species. The functional form of this equation is based on three commonly observed relationships regarding the density dependence of plant yield that are relevant for both weeds and crops. First, yield per unit area of a species in monoculture often has been observed to increase toward an upper asymptote as density of that species increases. Second, annual plant biomass and seed production ("yield") per plant are typically decreasing nonlinear functions of the density of other plants in the neighborhood. Third, yield per unit area of a species at a constant density tends to decrease toward a lower asymptote as the density of plants of competing species increases. These three relationships have often been described by a class of equations called "rectangular hyperbolic equations" or "reciprocal yield equations" (Pacala 1986; Pacala and Silander 1990; Watkinson 1981; Weiner 1982; Willey and Heath 1969). One useful form of a rectangular hyperbolic equation is:

$$R = U_R \cdot \frac{N}{N50 + N} \qquad [5]$$

where R is the response being measured, N is the independent variable, U_R is the upper asymptote as N approaches infinity, and N50 is a parameter indicating the level of N where R equals 50% of U_R (Figure 2).

Equation 5 can be used to describe crop yield in response to crop density or weed "yield" as a function of weed density. Equation 6 is for crop yield:

$$Y_{crop} = Y\max_{crop} \cdot \frac{N_{crop}}{N50_{crop} + N_{crop}} \qquad [6]$$

Similarly, Equation 5 also can be used to model the decreasing yield of a species in the presence of increasing density of a second species. In this case, R would refer to the amount of yield reduction (or "yield loss") of the species in the mixture compared to its yield at that density in monoculture. Then N refers to the varying density of another competing species, and the upper asymptote U_R gives the upper limit of yield loss that could be caused by a high density of the second species impacting on the first. Equation 7 is for crop yield loss in response to density of a single weed species:

$$YL_{crop} = YL\max_{crop} \cdot \frac{N_{weed}}{N50_{weed} + N_{weed}} \qquad [7]$$

However, the effect of weed density on crop yield is summarized more often using a different hyperbolic yield loss model (Cousens 1985a) given in Equation 8:

$$Yld = Ywf \cdot \left(1 - \frac{I \cdot N_{weed}}{\left(1 + \frac{I \cdot N_{weed}}{A}\right)}\right) \qquad [8]$$

where Yld is the crop yield as affected by presence of weeds, and Ywf, I, and A are fitted parameters, with Ywf indicating the average weed-free yield, I being related to the initial slope of the yield curve, and A being the asymptotic maximum proportional yield loss as weed density approaches infinity. Equation 8 is equivalent to Equation 7 when YL_{crop} = Ywf - Yld, $YLmax_{crop}$ = Ywf · A, N = N_{weed} and $N50_{weed}$ = A/I.

A simple variant of Equation 5 could be used to model crop yield in response to crop and weed density. This model for a single weed species is shown in Equation 9:

$$Y_{crop} = Ymax_{crop} \cdot \frac{N_{crop}}{N_{crop} + N_{weed} \cdot CI_{weed} + N50_{crop}} \qquad [9]$$

Here $Ymax_{crop}$ is the upper limit of crop yield as crop density approaches infinity and weed density is zero (like U_R in Equation 5), CI_{weed} is a fitted parameter which converts weed density into a number of "crop plant equivalents," and $N50_{crop}$ is a fitted parameter of intraspecific competition theoretically equal to the N50 value (Equation 5) for the crop in monoculture. The parameter CI is a crowding index which describes the intraspecific competitiveness of the weed compared to the intraspecific competitiveness of the crop, defined theoretically as the ratio $N50_{crop}/N50_{weed}$. Equation 9 is equivalent to Equation 6 if weed density is held constant.

We combined Equations 6 and 8 to derive our generalized equation for proportional yield loss. Crop yield in response to density of the crop and a single weed species is modeled as:

$$Y_{crop} = Ymax_{crop} \cdot \left(\frac{N_{crop}}{N_{crop} + N50_{crop}}\right) \cdot \left(1 - \frac{N_{weed} \cdot CI_{weed} \cdot A/100}{N_{weed} \cdot CI_{weed} + N_{crop} + N50_{crop}}\right) \qquad [10]$$

where all parameters and variables are as defined previously. Equation 10 is divided by $Ymax_{crop}$ for proportional yield loss. The first two components of Equation 10 represent the crop yield in monoculture (Ywf in Equation 8). The last component includes the parameter A of Cousens' (1985a) yield loss equation (Equation 8), and this component has the same role as the parenthetical expression in Equation 8. Equation 10 is equivalent to Equation 8 when crop density is constant and

$$Ywf = Ymax_{crop} \cdot \frac{N_{crop}}{N_{crop} + N50_{crop}} \qquad [11]$$

and

$$\frac{CI}{(N_{crop} + N50_{crop})} = \frac{I}{A} \qquad [12]$$

Canner et al. (2002) proposed an approximately linear replacement of lost crop yield by increases in weed yield for weeds and crops in mixtures and found that N50 for density-dependent weed seed production in the form of Equation 5 has a one-to-one correlation to N50 of a fitted curve describing crop yield loss as a function of weed density. This correlation suggests that a single set of parameter values can be used to describe the influence of weed density on crop yield and weed seed production. Also, a single set can describe the influence of crop density on crop yield and weed seed production. We used this relationship to derive our equation for proportional yield loss in WISDEM. Our equation for relative yield of both crop and weeds is:

$$PY_x = \left(\frac{N_x \cdot CI_x}{\sum_{k=1}^{x} N_k \cdot CI_k + N50_1} \right) \cdot \left(\frac{\sum_{k=1}^{x-1} N_k \cdot CI_k \cdot A'_k + N50_1}{\sum_{k=1}^{x-1} N_k \cdot CI_k + N50_1} \right) \cdot \left(1 - \frac{\sum_{k=x+1}^{n} N_k \cdot CI_k \cdot A'_k}{\sum_{i=1}^{n} N_i \cdot CI_i + N50_1} \right) \quad [13]$$

The density of each of *n* species in the system is $N_k = 1\ldots n$ and the parameters A'_k and CI_k describe differences in intraspecific and interspecific competitive ability among species. The parameter N50 is defined as in Equation 5 except the subscript 1 indicates that this is the N50 value for the most competitive species. All species are ranked by their interspecific competitive ability for this calculation with $x = 1$ for the species that is most competitive to $x = n$ for the least competitive species, where *n* is the number of species involved.

The first expression inside parentheses corresponds more or less to the monoculture yield component, similar to U_R in Equation 5. The major difference is that plants of any competitively superior species are also considered to have the same type of influence on this component of yield as are plants of the same species. The second parenthetical expression gives the "dominating" influence of competitively superior species ($k < x$), effectively giving the upper limit of the yield of species x as the density of species x approaches infinity. The third parenthetical expression is the "yield loss due to weeds" component. The numerator only includes competitively inferior species ($k > x$), whereas the denominator includes all species.

The density (N_k) in Equation 13 is defined as the number of competitive plants of other species. For simplicity, we do not consider competition from plants that are killed during the season. For weeds, $N_k = 1\ldots n$ is the number of plants present ($Nsurv_n$) the date of maturation of the weed (D_{wdmat}). For the crop, $N_k = 1\ldots n$ is the number of plants present on a fixed number of days after crop planting (D_{comp}) that is an estimate of the number of days after crop planting after which newly emerging weeds are believed to have minimal effect on final crop yield (Hall et al. 1992; Knezevic et al. 2002; Van Acker et al. 1993; Woolley et al. 1993)

The parameters A'_k and CI_k in Equation 13 are relative measures and are derived from two estimated parameters, N50 and A^0. Values of CI are calculated relative to the most competitive species, where $CI_k = N50_1/N50_k$. For crop–weed pairs where the crop is competitively superior to the weed, the calculated parameter A' in Equation 13 plays the role of A in Cousens' (1985a) model (Equation 8). Like Cousens' parameter A, A' is a measure of interspecific competition. It is the upper asymptote of yield loss of the more competitive species (usually the crop) as the density of the less competitive species (usually the weed) approaches infinity. Our parameter, however, is expressed as a proportion ($0 < A' < 1$) rather than as a percentage ($0 < A < 100$) and it is a calculated parameter that incorporates the effect of time of emergence on the maximum yield loss caused by weeds.

Yield Loss Equation: Time of Emergence. Most published data on the effect of emergence time are limited to single flushes of weeds that emerge after the crop. In contrast, WISDEM must be able to simulate effects of weeds that emerge over a range of times, including before the crop. Relative time of emergence has typically been modeled as having an impact on the initial slope of the yield loss curve (Parameter I in Equation 8; Cousens et al. 1987). However, our examination of a number of published studies indicate that maximum yield loss (e.g., the parameter A in Equation 8) decreases when weeds emerge after the crop emerges, so we focused on the influence of time of emergence on interspecific competition by adjusting the maximum yield loss a weed can cause. Our approach is similar to O'Donovan et al. (1985) but is based on a different equation. We do not adjust our CI_k for time of emergence because this is our measure of intraspecific competition.

WISDEM incorporates the impact of relative time of emergence on crop yield loss and weed yield by adjusting the value of A'. This adjustment occurs in three steps. The model begins with a parameter A^0 for each species in the model, which represents the relative interspecific competitiveness of the species. This parameter is adjusted for time of emergence of each individual plant relative to crop emergence, forming an intermediary number which we call A^*. From these individual plant values, we assign a value for the entire population of a species (A^*mean). Finally, A' for a species is derived from a ranking of the values of A^*mean of all species. These steps are described in more detail below.

The parameter A^0 is defined so that we can calculate a value of A' for any weed-crop combination, regardless of whether data are available to derive a parameter value for that specific weed in that particular crop. It is an estimate of the relative interspecific competitiveness of a species when the weed emerges with the crop. As a relative measure, A^0 is unitless and the scaling is arbitrary because it only indicates a proportional ranking between species. For example, if corn is thought to be twice as competitive another weed, the two values of A^0 for the species might be 1 and 0.5 or 2 and 1.

The A^* value given to a weed emerging on day d is modeled as a decreasing symmetrical logistic function of time in days L(d), with the point of inflection of L occurring at the date of emergence of the crop (D_{crem}):

$$A^* = L(d) = \frac{2 \cdot A^0}{1 + e^{(K \cdot (d - D_{crem}))}} \quad [14]$$

Table 2. Sources for estimated parameters of population change and yield loss in WISDEM.

Parameter Names	Literature sources	Expert opinion
Srv	Population decline experiments with 100% control	How long would it take to reduce population by half assuming 100% control? Srv would be calculated from the answer as the proportion surviving per year assuming exponential decline.
ReproMax	Weed population change data, carrying capacity data.	Not used
A^0	Experiments using Cousens (1985a) model	Expert ranking of competitiveness (adjusted to fit empirical data)
N50	Monoculture yield data, experiments using Cousens (1985a) model	Expert ranking of competitiveness (adjusted to fit empirical data)
$D_{wdstart}$, p1, p2	Published emergence curve data, fitted to Weibull function	Expert description of weed emergence curve, fitted to Weibull function
d_{crem}	Published data on time to crop emergence, sometimes in extension bulletins.	How many days typically elapse between planting and crop emergence?
D_{wdmat}	Not used	What is the average date when weed maturation and seed rain peaks?
POA	Published data on herbicide residual effect	How many days is this herbicide active in the soil?
eff	Colorado, Nebraska Extension Bulletins, Meister weed control guide	What percentage of plants would be killed by this management action?
K	Published data on effect of weed emergence time on crop yield loss, fitted to logistic function (specific to crop only)	Not used

We assume that the crop emerges on a single day. With A^0 as the baseline value of A^* for a given species when weed emergence occurs on the same day as crop emergence, K is a slope parameter. As d becomes early relative to crop emergence, A^* approaches $2 \cdot A^0$, and A^* approaches zero as d becomes late relative to crop emergence. The value of A^* for the crop is A^0 because we assume that the crop emerges all at once on one day. Because data for estimating L(d) are nonexistent for most crop and weed combinations, we assume a single value of K holds for all weeds growing with that crop.

We do not track of the A^* values of each individual plant. Instead, the sum of the A^* values of all the plants in a square meter of a given species is tracked. This sum is updated whenever new emergence occurs or when weeds are killed. The average value for all weeds of a given species, A^*mean, is calculated when it is needed to calculate proportional yield.

The values of A'_x are derived from a ranking of the values of A^*mean. All species are assigned a competitive rank index x based on descending order of their respective values of A^*mean, ranging from $x = 1$ for the species with the highest value of A^*mean to $x = n$ for the least competitive species, where n is the number of species involved. Then values of A'_x are created by dividing each A^*mean_x by A^*mean_1 (the highest value of A^*mean) and giving the most competitive species an A' value of one. Other A' values range between zero and one in proportion to their original A^*mean value.

Weed Emergence and Weed Control. The time of weed emergence is critical in computing both weed control and competitiveness. Weed emergence and weed control are calculated by a method similar to that of GWM (Wiles et al. 1996). Cumulative percent emergence is simulated over time for each weed species using a Weibull distribution based on julian days:

$$F(d) = 1 - \exp\left(-\left((d - D_{wdstart})/p2\right)^{p3}\right) \qquad [15]$$

where F(d) represents the proportion of total emergence having occurred by day d, $D_{wdstart}$ is the starting day of weed emergence, and p2 and p3 are fitted parameters. The total number of plants that have emerged by a given day is the cumulative percent emergence multiplied by $Npot_t$.

Herbicide applications, tillage operations, and the crop harvest are assigned a weed control efficacy, which is the percentage of the emerged weeds killed by the operation. Calculation of the number of weeds surviving control depends on whether the control is considered foliar active, soil active, or both. A tillage operation or a herbicide with foliar activity ("POST" control) kills weeds present at the time of application. The number of weeds killed is the efficacy of the control multiplied by the number of weeds emerged at that time and not yet killed by any previous control. Plants that have not emerged at the time of control are not affected, and continue to emerge normally after the control measure.

Soil-active herbicides only kill weeds that emerge during the herbicide's "period of activity" (POA). Plants that have emerged prior to the time of control are not affected. At the end of the POA, emergence proceeds normally. The POA for a soil-applied herbicide ends a specific number of days after the date of application. The number of weeds killed is determined by multiplying the control efficacy of the herbicide by the number of weeds that emerge during the POA. Some herbicides provide both kinds of control. That is, they will kill emerged weeds when they are applied, like a foliar-active herbicide, and they have residual activity that kills seedlings as they emerge, like a soil-active herbicide. WISDEM treats such herbicides as if both a "POST" application and a "SOIL" application occur on the same day.

Parameter Estimation. The parameters of the model can be derived entirely from literature sources and expert opinion (Table 2). All parameters in WISDEM are deterministic. Some parameters have alternative values based on whether there is irrigation or not, or whether the system is tilled. Generally, we used literature sources to estimate parameters with expert opinion used to fill in gaps. When several sources were available for the estimation of a parameter, a subjective "average" was selected, with a risk-averse bias toward making the weeds seem more damaging than they might be in reality.

Population Change Model. The parameters Srv (survival of the seed bank) and ReproMax (addition to the seed bank) can be estimated from a variety of sources. Both can theoretically be derived from estimates of their component parameters, β_{onsrv}, β_{offsrv}, β_{emg}, and MaxSeed. However, we found that observed values of ReproMax, and sometimes of Srv, appear to trend lower than would be estimated based on data from controlled experiments which measure the component parts.

Seedbank decline studies are common and were used to provide estimates of Srv when available. Srv is simply the rate of change of the population when there is 100% control.

Generally, an equation can be fitted to the seedbank decline data such that

$$N_t = N0 \cdot \exp(t \cdot \ln[Srv]) \qquad [16]$$

where N0 is the initial seedbank and t is the time in years. We used this approach; however, when data were not available, Srv was derived from similar parameters in the Dunan et al. (1996) model. Their parameters were based, at least in part, on a survey of expert opinion where a knowledgeable person would be asked to describe how long it would take to reduce a weed population of a given size to essentially zero, given 100% control; or how long it would take for a weed population to double, given zero control.

Ideally, ReproMax would come from observed data, where a given population of surviving plants produces a known number of offspring the following year. ReproMax is the most difficult of the parameters to estimate, but can be calculated from estimates of the more readily available parameters. Equation 4 can be solved to provide an estimate of ReproMax using data for population densities from two successive weed generations and estimates of other parameters. This appears to be the most reliable method of estimating this parameter and was used for obtaining preliminary estimates of ReproMax for several species in WISDEM. Typically, multiple estimates of this type were derived and a subjective "average" was used.

Similarly, ReproMax also can be calculated based on an estimate of the equilibrium density carrying capacity (Neq) of a species in a given situation, by setting $N_t = N_{t+1} = Neq$ and solving Equation 4 for ReproMax. This method was used to obtain preliminary estimates for a few weed species in WISDEM, using equilibrium densities from published data.

Yield Loss Equation. Whenever possible, we calculated A^0, the measure of relative interspecific competitiveness of a species, from values of A (Cousens et al. 1987) in the literature. Irrigated corn was assumed to be the most competitive species with $A^0 = 1$ (the highest value of A^0). Because values of A' in Equation 13 are obtained for species k by the ratio A_k^*/A_1^* (often the crop), the value of A^0 for a weed is found by adjusting A' in the literature for A^0 of the crop. Species not found in the literature were interpolated from calculated values based on expert opinion about the relative competitiveness of the weed species, such as the competitive indices used in herbicide decision models (Lybecker et al.1991; Wilkerson et al. 1991).

Values of N50 are needed for both crops and weeds. For crops, N50 can be estimated by fitting Equation 5 to commonly available data describing the effect of crop density on monoculture crop yield (Willey and Heath 1969), because it is the density at which plants of a species will produce half of their asymptotic maximum potential yield per unit area. It is assumed that N50 is roughly similar whether the data used to estimate it are from total crop biomass or crop grain yield.

Data describing the effect of weed density on crop yield are common, and often are summarized using the Cousens (1985a) hyperbolic yield loss model (Equation 8). Estimates of $N50_{weed}$ can be derived from published parameter estimates I and A given estimates of $N50_{crop}$ and the crop density (N_{crop}) in the experiment and these definitions:

$$CI = N50_{crop}/N50_{weed} \qquad [17]$$

$$A' = A/100 \qquad [18]$$

$$\frac{CI}{\left(N_{crop} + N50_{crop}\right)} = \frac{I}{A} \qquad [19]$$

By rearranging Equation 19 and making substitutions from Equations 17 and 18:

$$N50_{weed} = \frac{A \cdot N50_{crop}}{I \cdot \left(N_{crop} + N50_{crop}\right)} \qquad [20]$$

We used Equation 20 wherever possible to estimate N50. When published data were unavailable, N50 was estimated derived based on expert opinion of the relative competitiveness of weed species. We used this method because we found that literature-derived values of 1/N50 for weeds tended to be ordered similarly to values of A'.

The parameter for the number of days between crop planting and the date of yield loss calculation (d_{comp}), was derived from literature sources as the date after which weed removal does not improve crop yield and additional weed emergence does not reduce yield. The date of weed maturation (D_{wdmat}) was also based on published data, but there was large year-to-year variability in this date, so a subjective average was used. The parameter D_{crem} in Equation 14, the date of crop emergence, was calculated from experts' estimates of the days between crop planting and emergence (d_{crem} in Table 2). K was estimated for each crop species from one or more literature sources describing the effects of weeds over a range of emergence times.

Weed Emergence and Weed Control. The parameters of the Weibull function for modeling weed emergence ($D_{wdstart}$, p2, and p3 for Equation 15) were based on published data and were used whenever they were available. When expert opinion was used, experts were asked the relative magnitude of emergence during 1- or 2-wk intervals of a season. Herbicide efficacies were based on information from the latest Colorado and Nebraska weed control guides, whereas tillage and harvest efficacies are derived from the experience of several weed scientists. The period of activity of a soil-active herbicide was an estimate supplied by personnel involved in herbicide testing at Colorado State University.

Evaluation. WISDEM provides two critical outputs for the purpose of GPFARM: the population of each weed species in a given simulation year, and the crop yield loss caused by those weeds. These two components of the model were evaluated separately. Formal evaluation of our model was not possible with the limited number of appropriate data sets for multiple-species weed populations in general and more specifically for the Central Great Plains. Many available data sets were missing key information about weed densities or management. Moreover, with the small number of data sets, we had to use some of the data to calibrate and parameterize the model. Consequently, we evaluated our model for its intended purpose of decision support. Wilkerson et al. (2002) suggested that weed management decision models should be evaluated from three perspectives: Are the predictions biologically reasonable? Do the predictions help users make better decisions than they would otherwise? Is the model convenient and easy to use? Our evaluation addresses the first of these questions.

Table 3. Brief description of five data sources used in the evaluations.

Source(s)		Description	Treatments	Limitations
1	Daugovish et al. (1999); Lyon and Baltensperger (1995)	Dryland wheat, western NE, 6 yr	five crop rotations by three weed species	Only one weed species per treatment
2	Wilson (1993)	Irrigated corn, western NE, 4 yr, several weed species	eight weed management systems	
3	Moomaw and Martin (1984)	Irrigated corn, western NE, 3 yr, two weed species	five layby weed control treatments	Short duration, one of two weeds (large crabgrass) was not in WISDEM database.
4	Lyon, D. J. (personal communication); Kettler et al. (2000)	Dryland wheat-fallow, western NE, 6 yr, *Bromus tectorum* L.	six tillage systems by two rotation starting dates	All treatments have different initial weed pressures (due to history). Only one weed species
5	Schweizer and Zimdahl (1984)	Irrigated corn, northern CO, 6 yr, several weed species	four weed management systems	Full weed counts only available for two treatments

Our evaluation of the weed population dynamics component of the model consisted of demonstrating the ability of the model to fit five data sets that describe weed population dynamics over a period of years in response to crop management in the Central Great Plains region (Table 3). Published weed counts were compared to the predictions with WISDEM, based as much as possible on the available information on the crop management history. Data plots and descriptive statistics are presented. Because weed population demography involves the progressive multiplication of random events, it is reasonable to assume that errors will be larger as populations get larger, but might stay roughly in proportion to the size of the population. For this reason, a natural log transform of both observed and simulated values was used to evaluate the fit of the model. Also, this transformation gave a degree of normality and homoscedasticity to the data clouds. Correlation coefficients were computed between log-transformed observed and predicted values.

The data sources in Table 3 were not appropriate for evaluating the yield–loss component of the model because our model predicts yield loss as a percentage of weed-free yield. There were no independent estimates of weed-free yield in those data sets. For this evaluation, we compared parameters of a hyperbolic yield model fitted to data with parameters of a hyperbolic yield model fit to predictions generated with WISDEM. Data were collected from a number of sources describing crop yield loss over a range of weed densities (Table 4). The data were used to estimate parameters of the hyperbolic model:

$$\mathrm{Yld} = \mathrm{Ywf} \cdot \left(1 - \frac{\mathrm{N_{weed}} \cdot \mathrm{A}/100}{\mathrm{N50_{crop}} + \mathrm{N_{weed}}}\right) \qquad [21]$$

This model is equivalent to the Cousens (1985a) yield–loss model (Equation 8). If the published source presented model parameters for Equation 8, those parameters were converted to those of Equation 21 using the identity $\mathrm{N50_{crop}} = \mathrm{A/I}$. Data from rainfed areas in the United States and Canada east of 99° longitude were treated as if they were irrigated, whereas data from areas west of the 99° meridian were treated as dryland unless they were specifically irrigated. If the data sets included multiple emergence times, only the earliest weed emergence times were used. No adequate multiple-weed data sets were available.

The WISDEM module was run for similar scenarios, with a range of starting densities, in order to obtain WISDEM yield loss predictions for a range of weed densities to fit Equation 21. Because WISDEM's yield loss algorithm is based upon Equation 5, which is a hyperbolic model related to Equation 21, the hyperbolic model was always a perfect fit to the simulated yield loss outputs. The empirical model parameters were compared to the corresponding simulated model parameters for the same crop–weed pair to evaluate whether the simulated yield loss curve was reasonably similar to empirical outcomes.

Results and Discussion

Predictions of Population Change. The published studies we used for evaluation did not give clear initial estimates of weed population density prior to initiation of different treatments, thus it was difficult to estimate the initial weed population as required by WISDEM. This is a significant limitation to evaluation of WISDEM, especially for shorter-term data sets because sometimes data for the first 2 yr had to be used to estimate an initial weed population.

Plots of observed vs. simulated weed counts are significantly correlated for all data sets. Results for data sets 1 and 2 (Table 3) indicate that WISDEM is capable of generally simulating the influence of rotation and management on weed populations. Data set 1 (Daugovish et al. 1999; Table 3) included five crop rotations and data set 2 (Wilson 1993) included eight weed management systems. For the first data set, the plot of observed vs. simulated weed counts is strongly linear (Figure 3) with a correlation of $r = 0.903$ ($P < 0.005$). The same plot for data set 2 is quite spread out, but exhibits a trend along the one-to-one line (Figure 4). The observations are significantly correlated with $r = 0.448$ ($P < 0.005$). For both of these data sets, however, treatments with low weed densities were generally over predicted. Overprediction for low weed densities is also shown in the results for data set 3 (Moomaw and Martin 1984), but WISDEM lacked parameters for one of the species in this experiment (Figure 5). We simulated mixed populations of large crabgrass [*Digitaria sanguinalis* (L.) Scop.] and *Setaria* spp. as a population of only *Setaria* spp. The observed and simulated densities are significantly correlated with each other ($r = 0.591$, $P = 0.012$).

The simulated results for data set 4 (D. J. Lyon, personal communication; Table 3) have significant correlation to the observed results ($r = 0.588$, $P = 0.008$) but, in contrast to the results with the first three data sets, the fit was poorest at higher densities (Figure 6). This suggests that WISDEM might be missing some of the complex dynamics of the impact of tillage on weed populations because the treatments differed only in tillage systems, and downy brome (*Bromus tectorum*

Table 4. Data sources used in yield loss evaluation.

Source	Crop	Weed	Location[a]	Number of models[b]
Blackshaw 1993	Winter wheat, dryland	*Bromus tectorum* L.	Alberta, Canada	3
Blackshaw 1994	Winter wheat, dryland	*Bromus tectorum* L.	Alberta, Canada	12
Bosnic and Swanton 1997	Corn, rainfed	*Echinochloa crus-galli* (L.) Beauv.	Ontario, Canada	4
Cardina et al. 1995	Corn, rainfed	*Abutilon theophrasti* Medicus	Ohio	6
Cowan et al. 1998	Corn, rainfed	*Amaranthus* spp.	Ontario, Canada	4
		Echinochloa crus-galli (L.) Beauv.	Ontario, Canada	4
Dekker and Meggitt 1983	Soybean, rainfed	*Abutilon theophrasti* Medicus	Michigan	2
Dieleman et al. 1995	Soybean, rainfed	*Amaranthus* spp.	Ontario, Canada	4
Durgan et al. 1990	Sunflower, rainfed	*Kochia scoparia* (L.) Schrad.	North Dakota (East)	2
Fausey et al. 1997	Corn, rainfed	*Setaria* spp.	Michigan	2
Geier et al. 1996	Soybean, rainfed	*Helianthus annuus* L.	Kansas (East)	2
Harris and Ritter 1987	Soybean, rainfed	*Setaria* spp.	Maryland	3
Jasieniuk et al. 1999	Winter wheat, dryland	*Aegilops cylindrica* Host	Colorado	2
			Idaho	1
			Kansas (West)	3
			Montana	2
			Nebraska (West)	4
			Wyoming	3
Knake and Slife 1969	Corn, rainfed	*Setaria* spp.	Illinois	3
Knezevic et al. 1994	Corn, rainfed	*Amaranthus* spp.	Ontario, Canada	3
Knezevic et al. 1997	Sorghum, rainfed	*Amaranthus* spp.	Kansas (East)	3
Lindquist et al. 1996	Corn, irrigated	*Abutilon theophrasti* Medicus	Colorado	1
			Michigan	2
			Nebraska (East)	3
			South Dakota (East)	1
Massee 1976	Winter wheat, dryland	*Bromus tectorum* L.	Idaho	1
McGiffen et al. 1997	Corn, rainfed	*Setaria* spp.	Minnesota	14
	Soybean, rainfed	*Setaria* spp.	Minnesota	3
Miller[c]	Winter wheat, dryland	*Aegilops cylindrica* Host	Wyoming	1
Scholes et al. 1995	Corn, rainfed	*Abutilon theophrasti* Medicus	South Dakota	1
Smith et al. 1990	Sorghum, rainfed	*Echinochloa crus-galli* (L.) Beauv.	Oklahoma (East)	3
Stahlman and Miller 1990	Winter wheat, dryland	*Bromus tectorum* L.	Kansas	1
VanGessel et al. 1995	Corn, irrigated	*Amaranthus* spp.	Colorado	2
Wilson and Westra 1991	Corn, irrigated	*Panicum miliaceum* L.	Colorado	1
			Nebraska (West)	1
Zanin and Sattin 1988	Corn, rainfed	*Abutilon theophrasti* Medicus	Italy	2

[a] East/West indicates which side of the 99° meridian.
[b] Number of distinct model fits; typically from multiple sites or years.
[c] Source is http://www.ianr.unl.edu/jgg/projects/csuwfw.htm.

L.) the only weed in this experiment, is very sensitive to tillage systems.

The fifth data set, from an experiment with four weed management systems (Schweizer and Zimdahl 1984; Table 3), included many observed counts of zero. These are shown as 0.001 m^{-2} for the logarithmic scale of Figure 7. The correlation of observed and simulated escapes for these data sets was $r = 0.609$ ($P < 0.0001$). Without the zero counts, the correlation was $r = 0.628$ ($P = 0.001$).

Our evaluations included data from three experiments in irrigated continuous corn and two in dryland wheat-based systems. The model over-predicted yield loss at low densities in all of the irrigated continuous corn systems, but performed

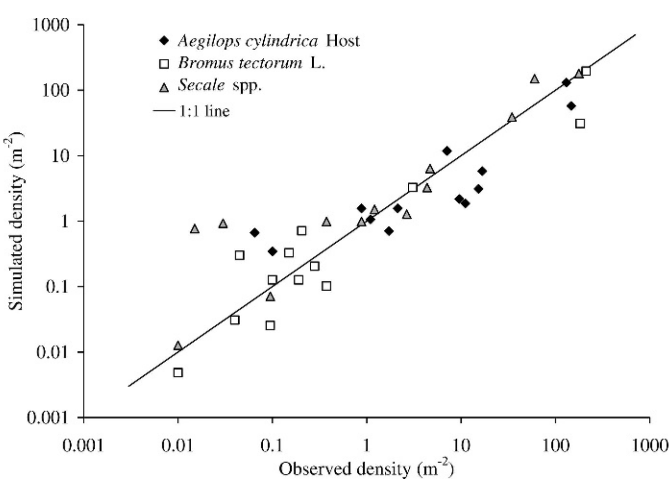

Figure 3. Results of validation for data set 1 (Daugovish et al. 1999; Lyon and Baltensperger 1995). The observed density and simulated density are correlated with $r = 0.903$ ($P < 0.005$).

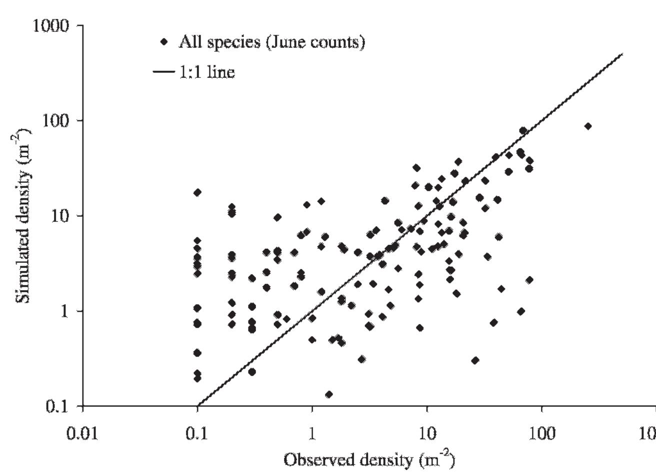

Figure 4. Results of validation for data set 2 (Wilson 1993). The observed and simulated density are correlated with $r = 0.448$ ($P < 0.005$).

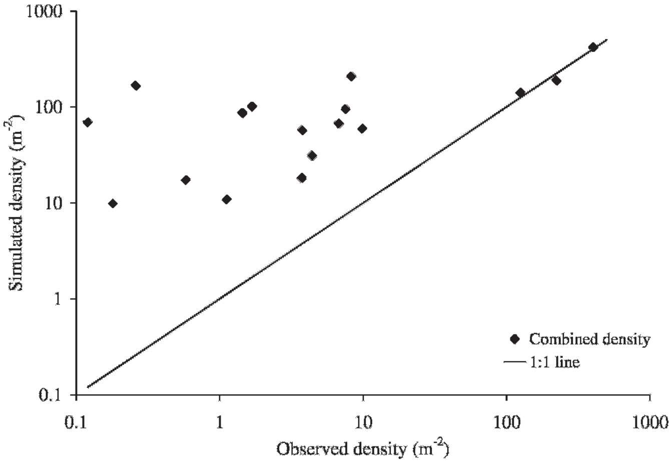

Figure 5. Simulated vs. observed density for validation data set 4 (Moomaw and Martin 1984). Because WISDEM does not have parameters for *Digitaria sanguinalis*, the simulation included only *Setaria* spp. and the evaluation results were compared to the sum of the observed densities of the two species. The observed and simulated density are correlated with $r = 0.591$ (P = 0.012).

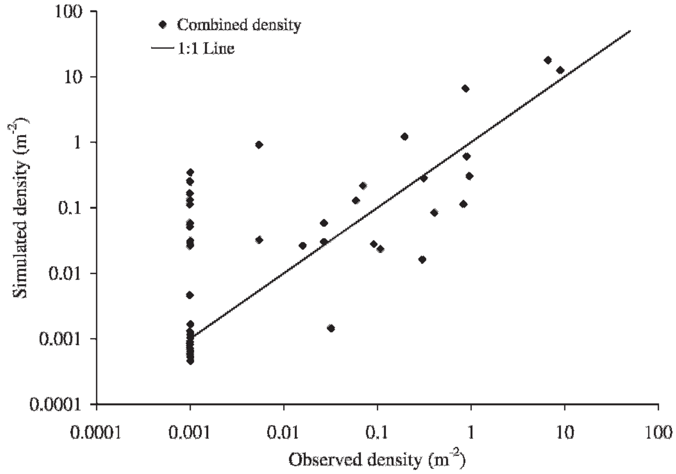

Figure 7. Simulated counts vs. observed counts for validation data set 3 (Schweizer and Zimdahl 1984). The observed and simulated density are correlated with $r = 0.609$ (P < 0.0001).

better with low densities in the dryland systems. The best results (data set 1) were in a system where the treatments were different crop rotations, whereas fits were poorer in systems emphasizing different weed management treatments such as tillage and/or herbicide systems. This suggests that the overall construction of the WISDEM model might be appropriate, but that implementation of weed control operations might require modification. Herbicide efficacy might be underestimated and we do not account for any effect of herbicides on size, seed production or competitiveness of escaped weeds (Adcock and Banks 1991; Kim et al. 2002).

Predictions of Crop Yield Loss. For crop–weed combinations where multiple empirical data sets were available, the model parameters A and N50 were summarized by averaging over all sites and years and computing the standard deviation (Table 5). The empirical N50 values corresponded reasonably closely with the WISDEM N50 values, with a correlation of $r = 0.81$, P = 0.0003 between the log transformed empirical N50 values and the log transformed WISDEM N50 values (Figure 8). For eight of 14 crop–weed pairs with estimates of the standard deviation of empirical N50 values, the simulated N50 value was within a range of plus or minus one standard deviation of the mean empirical N50 value. For 13 of the 15 (or 87%) crop–weed pairs, the simulated WISDEM N50 value was within a factor of four of the mean empirical value. Canner et al. (2002) suggested that N50 differences of less than a factor of five were probably within a reasonable range considering the natural variation in empirical N50 values.

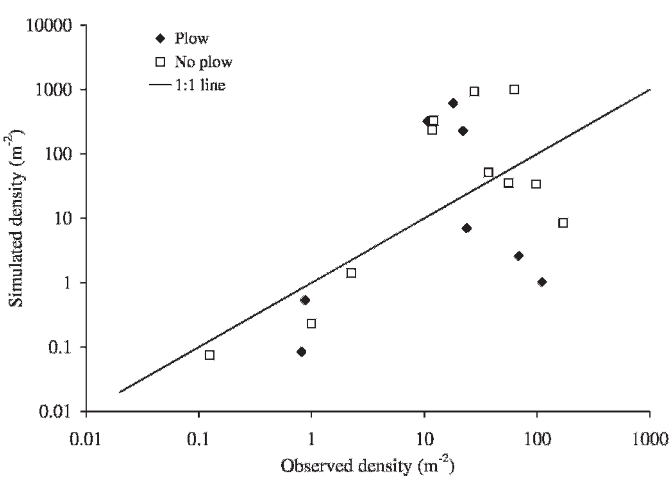

Figure 6. Simulated vs. observed density for validation data set 5 (D. J. Lyon, personal communication). The observed and simulated density are correlated with $r = 0.588$ (P = 0.008).

Among weed species represented more than once, both *Setaria* spp. and *Amaranthus* spp. appeared to have a consistent bias toward lower simulated N50 values than empirical values, whereas barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] and velvetleaf (*Abutilon theophrasti* Medic.) did not have consistent biases. This suggests that parameters for *Setaria* spp. and *Amaranthus* spp. could be adjusted somewhat to bring their simulation results more in line with empirical data.

Agreement between the simulated and empirical values is more difficult to assess for the parameter A than the parameter N50 because variation among empirical values of A for a crop–weed pair, shown by the standard deviations, was nearly as great as the variation among mean values of A for different pairs (Table 5; Figure 9). All but three of the empirical A values for a crop–weed pair were in the range of 50 ± 10%, whereas the average of the standard deviations for these mean values was 19.2%. Simulated and empirical values of A for all 15 crop–weed combinations were significantly correlated (P = 0.010) with $r = 0.64$. For eight of 12 of the crop–weed pairs with estimates of the standard deviation of the empirical estimates of A, or 67%, the simulated values of A were within one standard deviation of the mean empirical value. For 13 of 15, or 87% of the crop–weed pairs, the simulated value of A was within 20 percentage points of the mean empirical value. Although no consistent biases were apparent, the disparity between simulated and empirical values for *Amaranthus* spp. in irrigated soybeans was by far the largest, and merits further study.

Predicting for Decision Support. Weeds are controlled by strategic and tactical tools. We developed a simple model that predicts change in weed communities over years in response to tactical tools of weed management and crop rotation, an

Table 5. Results of comparing simulated yield loss curve parameters to empirical yield loss curve parameters.

Crop	Weed	Number of data sets	Empirical N50[a]	Simulated N50	Empirical A[a]	Simulated A
Corn	*Abutilon theophrasti* Medicus	16	8.9 ± 4.2	9.0	51.7 ± 20.1	60.6
Corn	*Amaranthus* spp.	1	4.8	3.1	51.6	49.6
Corn	*Echinochloa crus-galli* (L.) Beauv.	4	235.9 ± 152.8	72.0	54.1 ± 15.4	35.4
Corn	*Panicum miliaceum* L.	2	21.9 ± 6.4	13.1	52.0 ± 10.0	42.7
Corn	*Setaria* spp.	19	159.7 ± 119.8	58.5	48.2 ± 20.8	30.3
Sorghum	*Amaranthus* spp.	3	4.9 ± 1.9	3.6	43.7 ± 28.0	69.0
Sorghum	*Echinochloa crus-galli* (L.) Beauv.	3	9.6 ± 5.1	82.4	41.7 ± 12.6	55.5
Soybean	*Abutilon theophrasti* Medicus	2	5.2 ± 0.9	10.3	100	99.4
Soybean	*Amaranthus* spp.	8	9.8 ± 6.1	4.7	51.5 ± 31.6	98.2
Soybean	*Echinochloa crus-galli* (L.) Beauv.	4	91.5 ± 44.1	109.3	77.3 ± 19.5	66.3
Soybean	*Helianthus annuus* L.	2	1.6 ± 0.2	8.2	100	99.2
Soybean	*Setaria* spp.	4	160.6 ± 203.4	88.8	57.2 ± 31.6	59.2
Sunflower	*Kochia scoparia* (L.) Schrad.	4	1.9 ± 1.0	6.5	40.7 ± 5.1	54.8
Winter wheat	*Aegilops cylindrica* Host	16	23.1 ± 16.0	22.7	53.3 ± 22.2	55.8
Winter wheat	*Bromus tectorum* L.	17	67.3 ± 32.7	51.7	56.2 ± 19.1	37.3

[a] Mean ± standard deviation.

important strategic tool. Our simple model has many limitations for accurate predictions of long-term weed population dynamics. For example, the model does not respond to environmental conditions. Moreover, some weed scientists argue that predicting long-term population dynamics of weed populations is not possible (Cousens and Mortimer 1995). However, our goal was not long-term predictions but to allow consideration of weed population dynamics in strategic planning. We are not recommending a strategic plan but giving growers a tool to compare the influence of alternative management options on the weed population in a field.

Our goal was a simple model of weed population dynamics that could be parameterized with the limited data available in literature or with expert opinion rather than a detailed, mechanistic model. Lack of data or difficulty in observing certain processes of population dynamics mean that our model includes many simplifications of reality. For example, we do not attempt to estimate seed bank mortality by different causes and we assume emergence is independent of density. All our parameters are deterministic because we do not think there is enough information to describe relationships with environmental data and derive empirical distributions.

A more mechanistic model could lead to greater accuracy in predicting changes in weed populations if data were available for parameterization. Accurate predictions of weed biology are desirable for decision support systems, but accuracy is not the ultimate measure of their value. The value of decision support models is whether the user would make better decisions with the model than without the model. A more appropriate comparison in this case might be whether the user will make better decisions based on the dynamics of a single major weed or a weed community in a field. We sacrificed accuracy in predicting population change and yield loss for individual species to make predictions for weed communities. We tried to formulate a model from the general theory of density dependence of plant productivity for the most extensive use of limited information in the literature. We also tried to find sensible methods to use expert opinion in combination with these limited data.

Just as data are limited for developing and estimating parameters for models such as WISDEM, we lacked data for proper evaluation of WISDEM. In particular, we could not

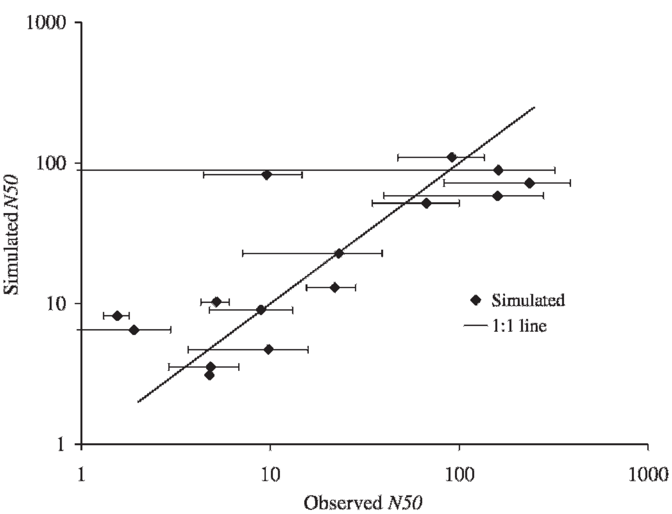

Figure 8. N50 values for simulated yield loss curves plotted against the mean of empirical N50 values for curves fitted to published research data. Standard errors are shown for observations when this statistic could be calculated. The observed and simulated density are correlated with $r = 0.807$ (P = 0.0003).

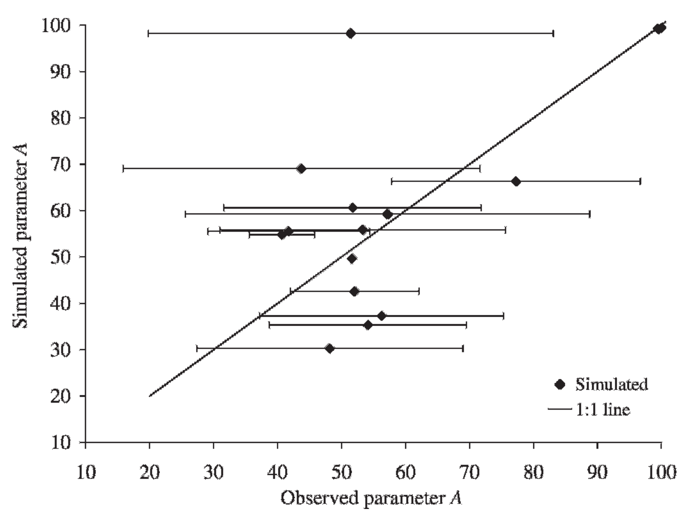

Figure 9. Values of parameter A for simulated yield loss curves plotted against the mean of empirical A values for curves fitted to published research data. Note that there are two points on top of each other at the upper right end of the line where both simulated and empirical A values were near 100%. Standard errors are shown for observations when this statistic could be calculated. The observed and simulated A values are correlated with $r = 0.641$ (P = 0.010).

find data to evaluate yield loss from multiple-species weed communities. Our limited evaluation provides some evidence that predictions of yield loss from single species of weeds and the short-term trajectories of changes in weed populations are biologically reasonable. Given the lack of data for further evaluation, the next step with this model is a sensitivity analysis to identify what information will best improve the value of the model for decision support.

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